

Species diversity and regeneration of old-growth seasonally dry *Shorea robusta* forests following gap formation

Indra Prasad Sapkota, Mulualet Tigabu, Per Christer Odén

Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, SE-901 83, Umeå, Sweden.

Abstract: Diversity and regeneration of woody species were investigated in two ecological niches viz. gap and intact vegetation in old-growth seasonally dry *Shorea robusta* (Gaertn. f.) forests in Nepal. We also related varieties of diversity measures and regeneration attributes to gap characteristics. Stem density of tree and shrub components is higher in the gap than in the intact vegetation. Seedling densities of *S. robusta* and *Terminalia alata* (B. Heyne ex Roth.) are higher in the gap than in the intact vegetation, while contrary result is observed for *T. bellirica* (Gaertn. ex Roxb.) and *Syzigium cumini* (L. Skeels) in term of seedling density. The complement of Simpson index, Evenness index, and species-individual ratio in the seedling layer are lower in the gap than the intact vegetation. Gap size can explain species richness and species establishment rate. Gaps created by multiple tree falls in different years have higher seedling density of *S. robusta* than gaps created by single and/or multiple tree falls in the same year. In conclusion, gaps maintain species diversity by increasing seedling density, and favor regeneration of Sal forests. In addition to gap size, other gap attributes also affect species diversity and regeneration.

Keywords: Canopy gap; intermediate disturbance hypothesis; Nepal; Sal (*Shorea robusta* Gaertn. f.) forest

Introduction

Understanding of canopy gap dynamics provides an insight into the many debated question whether or not species equilibrium is maintained in a forest community during regeneration processes in gaps (Barik et al. 1992; Zang and Wang 2002). Regeneration processes in gaps depend on several physical and biological factors involving canopy closure, intensive growth of advanced regeneration of pre-disturbance origin, and species colonization (Arriaga 2000). The prevailing regeneration strategy following a tree fall, including seed rain, seed bank, suppressed seedlings and saplings, vegetative regeneration, or lateral growth of peripheral trees, depends heavily upon the characteristics of gaps and disturbed areas (Runkle 1985; Lawton and Putz 1988; Brokaw and Scheiner 1989; Arriaga 2000).

The size of a gap, its temporal distribution, and severity of disturbance are the determining factors that account for changes in floristic composition, structure, species diversity, and regeneration. Tree fall gaps offer specialized regeneration niches as a

result of spatial and micro-environmental heterogeneity (Barik et al. 1992; Arriaga 2000; Li et al. 2005). Even within a gap, differences in light, moisture and temperature regimes and spatial heterogeneity caused by root, bole and crown zones, create a number of potential regeneration niches. Such heterogeneities are of fundamental importance in maintenance and promotion of high tree diversity in tropical forest communities (Connell 1978; Barik et al. 1992). Gap size is a critical variable for recruitment and establishment of different tree species (Brokaw 1985; Li et al. 2005). Regeneration strategy prevailing in small gaps is intensive growth of advanced regeneration (saplings), whereas the regeneration path in larger gaps is dominated by seed rain or seed bank of pioneer species (Runkle 1985; Garwood 1989). Small gaps are more likely colonized by clonal expansion of surrounding plants, whereas successful establishment through germination prevails in larger gaps (Bullock 2000), and establishment success from seed increases with distance to the gap edges (Li et al. 2005). Establishment of individuals in gaps depends not only on gap size, but also largely on how these gaps are created (Pakeman et al. 1998). Subtle aspects of tree fall gaps, involving shape (Li et al. 2005), age (Barik et al. 1992; Schnitzer and Carson 2001), number and causes of tree fall (Uhl et al. 1988; Arriaga 2000), gap canopy height and micro-environmental factors (Barik et al. 1992) are of equal importance for post-gap regeneration and diversity of tree species.

Despite a few studies in Indian sub-tropical region (Barik et al. 1992), southern tropics of India (Chandrashekar and Ramakrishnan 1993) and China (Zang and Wang 2002; Li et al. 2005; Zang et al. 2005) and temperate forests of Nepal (Vetaas 1997), the role of gaps in maintaining species diversity and regeneration in old-growth seasonally dry *Shorea robusta* forests (also known as Sal forests) in South East Asia is not fully understood. It is

Foundation Project: The study was supported by Swedish International Development Cooperation Agency (SIDA).

Received: 2008-08-27;

Accepted: 2008-11-25

© Northeast Forestry University and Springer-Verlag 2009

The online version is available at <http://www.springerlink.com>

Biography: Indra Prasad Sapkota (1970-), male, PhD. Forest ecologist, Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology, Tropical Silviculture and Seed Science Group, SE-901 83, Umeå, Sweden. E-mail: sapkotai@yahoo.com

Responsible editor: Hu Yanbo

also not apparent if gap disturbance regimes and regeneration processes in Sal forests are similar to those in tropical and temperate forests (Barik et al. 1992). In addition, selective logging of dead and diseased trees, a traditional management strategy in Nepal, has been in practice since the inception of local timber trade, which in turn results in formation of gaps in this forest type. Moreover, issues about conservation of biological diversity in Nepalese old-growth seasonally dry Sal forests have also been realized and substantial researches on forest management practices have been sought for.

Therefore, this study was conducted in Sal forests in Nepal with the following objectives: (1) to compare species diversity and regeneration between gap and intact vegetation environments; (2) to examine the relationship between gap attributes and species diversity and regeneration. This paper specifically sought to answer the following questions: (1) does gap environment favor herb, shrub and tree species recruitment and diversity? (2) If yes, which gap-built characteristics are the most influential factors affecting species recruitment, establishment and diversity?

Materials and methods

Study area

The study was conducted in State-owned seasonally dry Sal forests of Nawal Parasi district, located between 27°37.5' N and 84°3' E at ca. 190 m above sea level (Fig. 1). This forest type was chosen as it is the best representative of Sal forests in Nepal, which extends continuously from east to far west along the national highway. It covers an area of approximately 1000 ha and is considered to be one of the largest chunks of Sal forest in the locality. Due to poor protection and surrounding settlements, the entire forest experiences similar anthropogenic disturbances (e.g. fuel-wood, fodder and litter collection; moderate grazing pressure and encroachments etc.). No major natural disturbances (e.g. fire, hurricane and floods) across the entire forest were recorded.

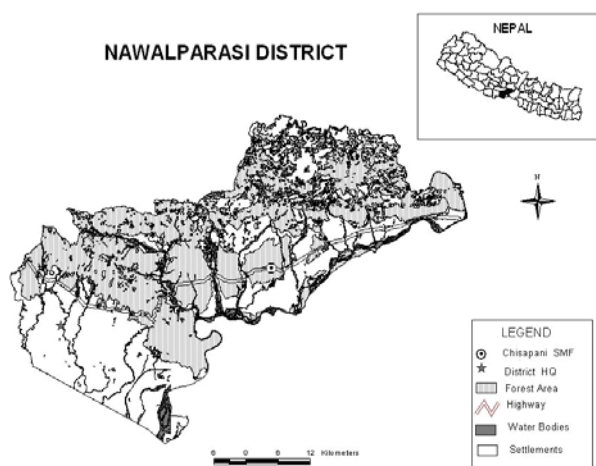


Fig. 1 Location of study area.

The geological formation of the study area is composed of coarsely bedded stones, crystalline rocks, clays and conglomerates (Anonymous 1994). Soil physico-chemical properties and some biological attributes of the forest are given in Table 1. The climate is tropical to sub-tropical with three distinct seasons: cold, hot and rainy. May and June are the hottest months with highest mean maximum temperature, and December and January are the coldest months. The maximum rainfall occurs during the monsoon season (June–September) and dew falls from December to February (Fig. 2).

Table 1. Summary of stem inventory and soil analysis of the study area, in State-owned seasonally dry Sal forests of Nawal Parasi district, located between 27° 37.5' N and 84°3' E at ca. 190 m above sea level.

Biological attributes	Mean values	Physico-chemical attributes	Mean values
Seedling density	54234/ha	Soil pH	5.5
Sapling/pole density	2720/ha	Organic matter	2.0 %
Sapling/pole basal area	3.4 m ² /ha	Moisture content	11.1 %
Canopy tree density	54/ha	N	0.347 %
Canopy tree basal area	15.8 m ² /ha	P	26.1 kg/ha
		K	471.2 kg/ha

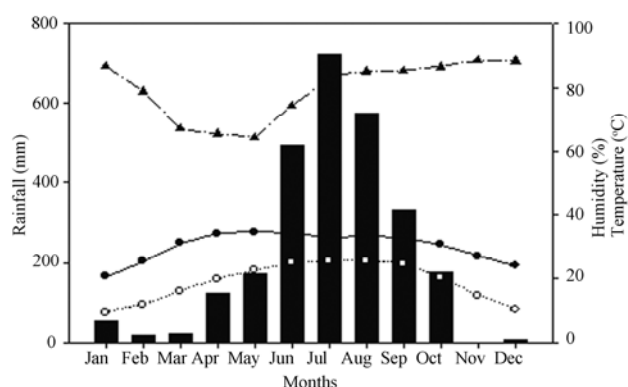


Fig. 2 Rainfall, relative humidity and temperature data for the study area in Sal forests in Nepal during January to December (mean of years 2003–2005); (vertical bars) average rainfall; (triangles) relative humidity; (points) mean maximum temperature; (circles) mean minimum temperature

Data collection

The present study was based on both natural and artificial canopy gaps formed through whole tree fall. The artificial tree fall refers to selective felling carried out either by the Department of Forests or illegal loggers. In our study, a gap is defined as an area larger than 25 m² opened by removal of canopy trees, where most of the living plants in gaps are less than 5 m tall and less than 50% of the height of the surrounding canopy trees (Lawton and Putz 1988). A gap also included both canopy gap and extended gap (Runkle 1982). The canopy gap refers to a hole from

the canopy down to the ground, and extended gap refers to the space enclosed by surrounding trees around the canopy gap. We define intact vegetation as an area with ca. 100% closed canopy as measured by densiometer.

The highway and its midpoint were taken as a reference for gap and intact vegetation survey because the highway divides the forest into two blocks. Six directions (20°, 50°, 110°, 240°, 250°, and 320°) were chosen based on field reconnaissance and visual interpretation of satellite images, and three arbitrary transect lines on either side (20°, 50°, 110° and 240°, 250°, and 320°) of the national highway were laid from midpoint of the highway in order to cover the entire core zone of the forest. The arbitrary transect lines with 40 m width were laid by five crew members walking 10 m apart from one another. Each transect was simply followed until 10 gap and intact vegetation spots were encountered. Spots in the intact vegetation were situated close to gaps (5–50 m away from a random border tree of each gap) to ensure similar topographical characteristics between them. A total of 60 gap and intact vegetation spots, 10 spots per transect line, were identified, labeled with paint and given serial numbers.

For each gap as an ellipse, its long axis and perpendicular short axis were measured to calculate the gap area. Trees, larger than 20 cm in diameter at breast height (DBH) on the edge of each gap, were identified at species level and their dbh was measured. Species names, stump diameter, and state (live or dead) of gap makers (trees with ≥ 20 cm stump diameter creating a gap) were recorded. Mortality types, i.e., standing dead, trunk broken or uprooted, of gap makers were noted. The cause of death and decay of each gap maker in each gap was recorded. Gap age classes were estimated by visual comparison of the decay classes of gap makers and the decay classes of known (with help of office records or persons involved in logging operation) log remains and stumps after cutting from nearby areas. Experienced local forest workers were also involved in estimating the ages of each gap maker. This approach of age estimation has successfully been used previously (Barik et al. 1992; Zang and Wang 2002). In case of multiple tree fall gaps, we assigned the oldest gap maker as key determinant of gap age and cause of tree fall, since we considered this as gap origin (Zang and Wang 2002). However, the gap formation events were described by combining number of tree falls and gap age. For example, we assigned a ‘single event gap’ if a single or multiple tree fall occurred in the same year. When the gap was formed with multiple tree falls in different years, it was assigned as ‘multiple event gap’. In order to avoid spatial autocorrelation and combined effects of two gaps along transects, a minimum distance of 100 m between successive border trees of sampled gap spots was maintained.

Detailed inventories in each gap and intact vegetation spot were carried out from November 2006 to March 2007 using the quadrat method. A 5 m \times 5 m quadrat was laid at the middle of each gap and intact vegetation spot. We made some alignment of quadrat at the intact vegetation spots with complete canopy closure. We also assigned nested 4 m² subquadrats at the corner of each 25 m² quadrat. Within the subquadrats (4 m²), all woody individuals with height between 10 cm and 200 cm were identi-

fied at species level and counted. Based on species growth form, we categorized species as tree, shrub or herb. Height and collar diameter of the tallest and shortest trees and shrubs were measured. Within the quadrats (25 m²), individuals with height more than 200 cm were identified at species level and their dbh was measured. Based on height of each individual, we grouped tree species into seedlings (individuals with height between 10 cm and 200 cm) and saplings (individuals with height more than 200 cm). The mechanism of natural regeneration (seed vs. vegetative) at the seedling layer were identified for all species, mostly through their morphological appearances; in some cases below-ground analysis of roots was also performed. Identification of species was made *in situ* when possible, and by comparison with voucher specimens of the National Herbarium. The sterile specimen vouchers of these species were deposited in the District Forest Office.

Data analyses

In order to permit a more precise comparison of alpha diversity in the gap and intact vegetation, a variety of commonly used diversity indices were computed based on the total number of species and individuals for each growth form. The indices were as follows:

Margalef's index of species richness,

$$D_{mg} = (S - 1) \ln N \quad (1)$$

Shannon-Wiener index,

$$H' = -\sum p_i \log_2 p_i \quad (2)$$

Simpson's index,

$$D = \sum (n_i(n_i - 1) / (N(N - 1))) \quad (3)$$

Shannon's measures of evenness,

$$J' = H' \ln S \quad (4)$$

Fisher's index of diversity,

$$\alpha = N(1 - x) / x \quad (5)$$

where, S , N , p_i , n_i and x are the total number of species, total number of individuals, the proportion of individuals found in the i th species, the number of individuals in the i th species, and the log series parameters, respectively.

Species-abundance curves were plotted using overall density (log value) of herbs, shrubs and trees against its corresponding species sequence in order to interpret the community organization in terms of resource share and niche-space (Pande 1999). Plot level density of each growth form, *S. robusta* seedling population (seed vs. vegetative), population of socio-economically important tree species, sapling population (*S. robusta* vs. other species) and diversity indices were calculated and compared between the gap and the intact vegetation using paired sample t-test. The missing values were replaced by means (Tabachnick and Fidell 2001). Establishment rate for any given

species was computed as ratio of the density of seedlings to that of saplings. Gap attributes, i.e. gap size, number of fallen trees, gap age, tree fall basal area and basal area of border trees were related to the dependent variables (i.e. species richness, diversity, evenness, establishment rate of *S. robusta*- and other species) using Pearson correlation. The mid values of gap age classes were used to analyze its association to various dependent variables (Tabachnick and Fidell 2001). The effect of gap formation events (single vs. multiple) on species richness, diversity, evenness, *S. robusta* seedlings and other seedlings were compared using independent sample t-test. Prior to analysis, the data sets were either log- or square root transformed as deemed necessary in order to normalize the data sets. All analyses were done using SPSS version 14 (SPSS for Windows, Chicago: SPSS Inc.).

Results

Species diversity

A total of 4041 individuals belonging to 48 species were encountered in 120 sample plots (Table 2). Among the 48 species, 43 species were recorded in the gap and 37 species were recorded in the intact vegetation environment. The species abun-

dance patterns of each growth form as well as the whole vegetation community displayed a typical reverse J-distribution or log series distribution for both the gap and intact vegetation environments (Fig. 3), where the majority of the species had few individuals and minority species had many individuals. However, many herbs and trees had low species abundance in the gap, while many shrubs with few individuals were found in the intact vegetation.

The various diversity indices for each growth form did not vary consistently between the gap and intact vegetation (Table 2). For herbs and trees, the total number of species (S), species richness (D_{Mg}), and Fisher's diversity index (α) were slightly higher in the gap than in the intact vegetation, while the above three indices for shrub were slightly higher in the latter. The total number of individuals (N) for all the three growth forms was higher in the gap than in the intact vegetation. The species turnover rate, as measured by numerical species richness (S/N), was higher in the gap for herbs and in the intact vegetation for shrubs, and approximately the same in both environments for trees. The Shannon-Wiener index (H'), the complement of Simpson's index ($1 - D$) and the Shannon's measure of evenness (J') was slightly higher in the intact vegetation than in the gap for shrubs and trees while nearly the same for herbs.

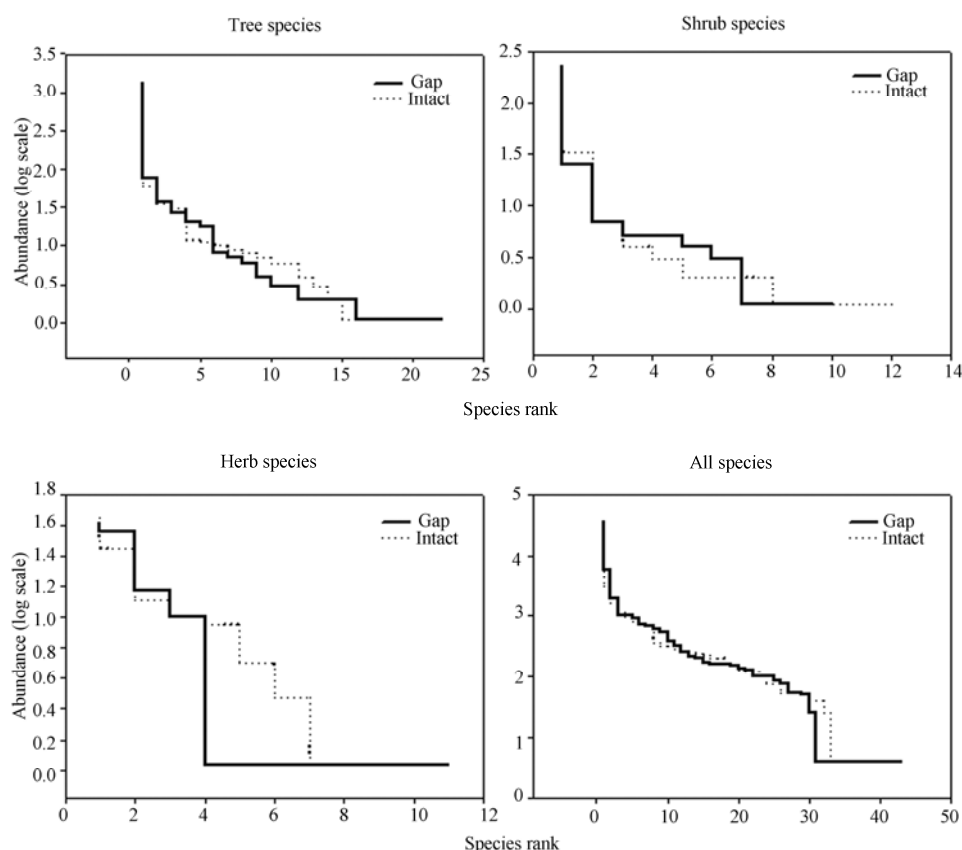


Fig. 3 Species abundance curves for the gap and intact vegetation in State-owned seasonally dry Sal forests of Nawal Paransi district.

At plot level, complement of Simpson index ($t [59] = 2.1$; $p = 0.048$), Shannon's evenness index ($t [59] = 3.5$; $p = 0.001$) and species-individual ratio ($t [59] = 4.6$; $p < 0.0001$) in the seedling

layer were significantly lower in the gap than in the intact vegetation, while no differences were found in species richness and Shannon-Wiener index. The species richness of the sapling

population was not significantly different between the gap and intact vegetation (Fig. 4).

Table 2. Species diversity indices of different growth form in the gap and intact vegetation environments in Sal forests in Nepal.

Stand attributes	Diversity indices							
	<i>S</i>	<i>D_{mg}</i>	<i>N</i>	<i>S/N</i>	<i>H'</i>	<i>1-D</i>	<i>J'</i>	<i>α</i>
Herbs								
Gap	11	2.12	110	0.100	2.276	0.733	0.94	10.36
Intact	8	1.28	105	0.056	2.148	0.718	1.10	4.18
Shrubs								
Gap	10	1.54	346	0.028	1.628	0.492	0.70	5.34
Intact	12	2.09	189	0.063	2.113	0.620	0.85	8.90
Trees								
Gap	22	2.77	1958	0.011	0.967	0.240	0.31	9.54
Intact	19	2.36	1333	0.013	1.391	0.360	0.48	8.04
Total								
Gap	43	5.39	2414	0.018	2.066	0.515	0.55	21.65
Intact	37	5.00	1627	0.022	2.502	0.601	0.69	19.02

S is the total number of species recorded, *D_{mg}* the Margalef's index of species richness, *N* the total number of individual enumerated, *S/N* the rate of species increase per individual enumerated, *H'* the Shannon-Wiener index, *1-D* the complements of Simpson's index, *J'* the Shannon's measures of evenness, *α* the Fisher's index of diversity.

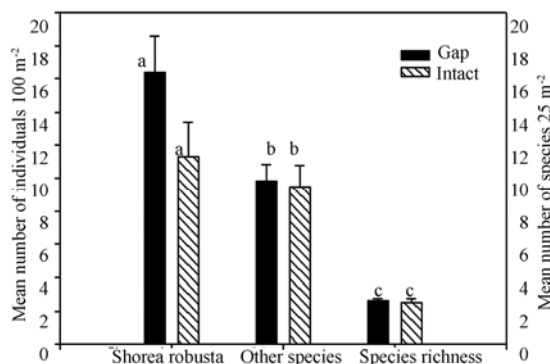


Fig. 4 Species richness and density of sapling populations in the gap and intact vegetation. The different letters show significant differences ($p < 0.05$; pair-wise t-test).

Regeneration

Seedling recruitment differed significantly between the gap and intact vegetation, depending on growth forms (Table 3). The number of seedlings for tree and shrub was higher in the gap than in intact vegetation, but no difference was found in the number of seedlings for herb between the two environments. At individual species level, higher seedling densities of *S. robusta* and *Terminalia alata* were observed in the gap than that in the intact vegetation, while that of *Terminalia bellirica* and *Syzgium cumini* were higher in the intact vegetation than in the gap (Table 4). Analysis on the mechanism of natural regeneration of the dominant species, *S. robusta* revealed that the density of vegetatively recruited individuals was significantly higher in the gap than in the intact vegetation, while no significant variation in the

density of seed-originated seedlings was observed between the two environments (Fig. 5). The sapling density of *S. robusta* as well as other species had no significant difference between gap and intact vegetation (Fig. 4).

Table 3. Number of seedling and saplings (mean \pm SE) of different growth forms in the gap and intact vegetation environments (100 m²).

Growth form	Number of seedling and saplings		t-statistic	df	P-value
	Gap	Intact			
Trees	871 \pm 33	578 \pm 28	6.45	59	0.000
Shrubs	150 \pm 13	93 \pm 9	3.71	59	0.000
Herbs	87 \pm 9	75 \pm 5	1.31	59	0.193

Table 4. Number of individuals (mean \pm SE) of six socio-economically important tree species in the gap and intact vegetation environments (100 m²). Fo, Fu, T and M refer to as fodder, fuel wood, timber and medicine, respectively.

Species	Major use	Number of individuals		t-statistic	df	P-value
		Gap	Intact			
<i>S. robusta</i>	Fo, Fu, T, M	595 \pm 32	362 \pm 23	5.9	59	0.000
<i>T. alata</i>	Fo, Fu, T, M	38 \pm 2	18 \pm 1	9.8	59	0.000
<i>T. bellirica</i>	Fo, Fu, M	17 \pm 0.5	31 \pm 1	17.7	59	0.000
<i>S. cumini</i>	Fo, Fu, T, M	32 \pm 1	72 \pm 8	5.2	59	0.000
<i>E. operculata</i>	Fo, Fu, T, M	34 \pm 2	45 \pm 7	1.5	59	0.133
<i>L. parviflora</i>	Fu, T, M	8 \pm 1	8 \pm 1	0.04	59	0.972

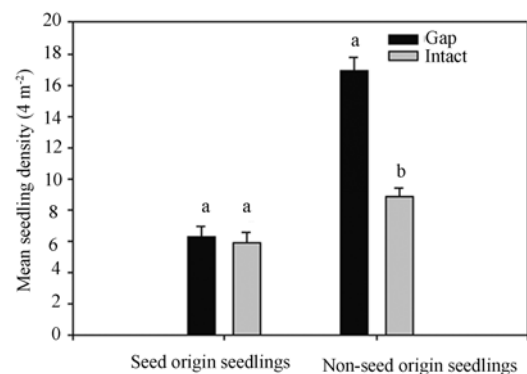


Fig. 5 Mechanisms of natural regeneration (seed origin seedlings and non-seed origin seedlings) of *Shorea robusta* in the gap and intact vegetation. Nested 4-m² subquadrats were assigned at the corner of each 25 m² quadrat. The different letters show significant differences ($p < 0.05$; pair-wise t-test).

Relationship between gap characteristics and vegetation attributes

In general, the correlations between various vegetation attributes and gap characteristics were weak, except for several exceptions (Table 5). For instance, a significant and negative association existed between species richness and gap size and basal area of border trees. Shannon diversity index and evenness showed a significant positive relationship with basal area of fallen trees.

Moreover, the establishment rate of *S. robusta* showed a negative relationship with number of fallen trees while the establishment rate of other species had a negative relationship with gap size and basal area of border trees. Gap formation events did not affect diversity indices as well as overall seedling density of all species other than *S. robusta* that had a higher mean seedling density in gap created by multiple tree falls in different years than that in gap created by single tree fall and/or multiple tree falls in the same year (Table 6).

Table 5. Correlation (r) of diversity indices and regeneration attributes with gap plot characteristics (n = 60).

Vegetation attributes	Gap plot characteristics				
	Gap area (log ₁₀)	Number of tree fall	Gap age	Border basal area	Tree fall basal area
Species richness	-0.287*	0.181	0.110	-0.463**	0.037
Shannon index	-0.086	0.210	0.174	-0.218	0.259*
Evenness	0.086	0.211	0.200	-0.051	0.280*
^a Establishment rate (<i>Shorea robusta</i>)	0.164	-0.288*	-0.109	0.131	0.026
^a Establishment rate (other species)	-0.261*	-0.001	-0.036	-0.309*	-0.109

**, * p values <0.01; <0.05; ^a Square root transformation

Table 6. Plot-wise values (mean ± SE) of different vegetation attributes and t-statistics of single and multiple tree falls in different time series of the gap formation phase.

Vegetation attributes	single event (n = 42)	multiple event (n = 18)	df	t-statistics	P-values
Species richness	6.3±33	7.2±0.6	58	1.37	0.175
Shannon index	1.48±.05	1.46±0.13	58	0.16	0.868
Seedling density (100 m ²)	0.56±0.02	0.50±0.06	58	1.13	0.262
Seedling density (100 m ²) (<i>Shorea robusta</i>)	549±6	725±80	58	2.91	0.005
Evenness(other species)	275 ± 17	276 ± 22	58	0.04	0.967

Discussion

The present study shows that majority of the species have few individuals and minority species have many individuals in both gap and intact vegetation environments. This characteristic coincides with the reverse J-distribution or log series distribution of species-abundance curve that is a typical characteristic of many old-growth forests in the tropics (Pitman et al. 1999; Huang et al. 2003). Similar observation has been made by Pande (1999) in some disturbed *S. robusta* forests in India. Log series distribution maintains a moderate size of common and few abundant species (Pande 1999). This pattern of distribution suggests that a post-gap forest community in Sal forests maintains relatively heterogeneous assemblages of species (Pande 1999; Behera and Misra 2006).

Our finding is consistent with other reports that tree species richness is higher in the gap than in the intact vegetation (Runkle 1982; Denslow 1995; Zang and Wang 2002; Li et al. 2005). Generally gaps maintain species diversity by providing colonization sites for shade intolerant, pioneer species in the community (Clarke and Allaway 1993; Dalling et al. 1998), and by increasing tree establishment, and thus stand density, which in turn can lead to higher tree species richness (Denslow 1995). Tree fall gaps generally produce environmental heterogeneity, which ensure different light, temperature, moisture and/or nutrient regimes that trigger germination and growth (Denslow 1995). In some cases, the increase in diversity caused by gaps would simply be a transient effect of increased density and would disappear following thinning (Denslow 1995; Gotelli and Graves 1996; Hubbell et al. 1999; Stevens and Carson 1999). The high seedling density in gaps could explain the slight increase in overall diversity (Fisher's index in particular) in gaps observed in the present study.

Our regeneration data showed extremely high seedling densities of trees and shrubs in the gap, which is consistent with findings reported by Bertrand et al. (1995) in the desert, Chambers (1995) in alpine tundra and Whitmore (1989) in tropical forests. Generally, regeneration processes in gap depend on several physical and biological factors (Arriaga 2000). Canopy gaps are always found to have higher light intensities at soil surface and hence often higher soil temperature than closed vegetation (Denslow et al. 1998). Moreover, competition for one or more resources (e.g. light, nutrients, and water) is less in canopy gaps than in intact vegetation (Bullock 2000). Thus, the combined effect of increased light intensity, increased soil temperature and reduced competition increases seedling recruitment and establishment in canopy gaps compared to closed canopies.

The mechanism of seedling regeneration also has a strong influence on the gap colonizing ability of the species. For example, the density of seed-origin seedlings of *S. robusta* did not differ between the gap and intact vegetation while the density of vegetatively recruited individuals was favored by the gap. This can be related to the seed availability, resprouting ability of the species and gap size. Generally, *S. robusta* has a low seed availability due to a long seed period for normally every third year (Gautam and Devoe 2006), short seed viability (Jackson 1994) and often seed collection by local people for its immense economic value. The low seed availability could influence the recruitment of seed-origin seedlings. Vegetation cover in gaps is often maintained by prolific ramet producers, especially through rhizomes or resprouts as disturbance-led openings accelerate these processes (Pandey and Shukla 2001). *S. robusta* is a prolific resprouter and the resprouts of the species develop slowly in shade compared to in the open, which in turn leads to lower survival rate under closed canopy (Rautiainen and Suoheimo 1997). Small gaps more likely favor clonal expansion of surrounding plants, whereas large gaps favor successful establishment through seed germination. Also, the establishment success from seed increases with distance to the gap edge (Li et al. 2005).

A rapid recruitment of pioneer shrubs following gap formation is another important factor accountable for high seedling density

in canopy gaps (Deb and Sundriyal 2007). In the present study, *Clerodendron viscosum* – a nurse shrub for natural regeneration of *S. robusta*, was found in substantially higher density in canopy gaps (98 individuals per 100 m²) than in intact vegetation (45 individuals per 100 m²), thus resulting in higher density of the shrub population in the gap. The lack of significant variation in herb density between the gap and intact vegetation could be related with reduced availability of light due to overshadowing by the dense population of shrubs and trees as well as competition for other resources (Yu et al. 2006).

The lack of significant difference in stem abundance and species richness of sapling population between the gap and intact vegetation corroborates with findings of Uhl et al. (1988), Hubbell et al. (1999) and Babaasa et al. (2004). In an old-growth tropical forest, the gap disturbance regime actually did not control the variation in tree diversity and density of advance regeneration (Hubbell et al. 1999). It is so because: (i) gaps remained dominated by shade-tolerant tree species of advance regeneration (saplings) before gap formation (Uhl et al. 1988), which results in similar post-gap abundance and diversity pattern; and (ii) physical damage during the tree fall and removal events might reduce their density in the gap.

The correlation analysis between gap plot characteristics and vegetation attributes revealed a negative relationship between gap size and species richness, which further supports the significantly higher diversity observed in the intact vegetation than in the gap. Increase in gap sizes can change markedly the extreme values of microclimate (Whitmore 1996), and lower the survival and growth of recruits, particularly in dry forests. An increase in Shannon index and evenness with increasing tree fall basal area suggests that colonizers can obtain increased space by big-sized tree fall, and invade into and grow in the new habitats (Li et al. 2005). Apparently, bigger pre-gap canopy trees produced larger tree fall basal area. Before gap creation, these trees shaded the entire micro-sites and maintained relatively even distribution of shade-tolerant species (Uhl et al. 1988), which is exemplified by the shade tolerant of species (Jackson 1994). Our study shows that *S. cumini*, *Eugenia operculata*, *T. bellirica*, *Semecarpus anacardium* have significantly higher seedling density in the intact vegetation than in the gap.

The multiple gap makers with successive gap events favored early recruitment (seedling) of *S. robusta*, which can be attributed to rapid successional recovery of the *S. robusta* population (Webb and Sah 2003) due to continuous light availability (Gautam and Devoe 2006), increased photosynthesis and increased ground temperature (Li et al. 2005). However, the negative relationship of *S. robusta* establishment rate with number of tree falls can be attributed to logging effects as multiple tree falls at a single event (e.g. wind fall) followed by logging operations physically damage saplings but accelerate post-logging regeneration of *S. robusta* (pers. obs.).

We find significant negative association of species richness and establishment rate of other species with basal area of bordering trees, perhaps due to pests (Richards and Coley 2007) and/or root competition (Brokaw 1985). In general, most of the tree species are susceptible to insect attacks and diseases. How-

ever, shade-tolerant species are more susceptible and therefore suffered severe stress in larger gap as observed by Tabarelli and Mantovani (2000) in south eastern Brazil. Big-sized (old-growth) trees around the gap might serve as host trees for different herbivores (e.g. ants, termites, grasshoppers; pers. obs.), which feed on seeds or young leaves of seedlings and therefore lowered the density and diversity at recruitment stage. Moreover, old-growth trees around the gap might also enhance seedling mortality due to root competition between seedlings and bordering trees for nutrient and water. Richards and Coley (2007) reported that plants, young leaves, herbivores and predators were significantly more abundant in larger gap than elsewhere in the community. Similar conditions might exist in our study site, where a majority of species (*ca.* two-third of referenced) were characterized as shade-tolerant (Jackson 1994), explaining the inverse relationship between gap size and establishment rate of other species.

In conclusion, the results show that gaps maintain overall species diversity through an increase in total density without having an effect on density of saplings. Gaps in old-growth Sal forests improve regeneration of various tree species, but resulted in higher dominance of *S. robusta*. Larger gaps tend to lower species equilibrium. The results also highlight that not only gap size but also other gap attributes have an influence on post-gap regeneration and diversity.

Acknowledgements

We thank Bijaya Raj Paudel and Padam Prasad Nepal for their help with logistics. We are grateful to Shesh Kanta Bhandari, Bishnu Bahadur Thapa, Shyam Sundar Bhandari and Tek Bahadur Rayamajhi for their constant support during the forest inventory. Meena Kunwar and Poorneshwor Subedi provided the satellite images. We also thank Chaudhary, Dr. Sushim Ranjan Baral and Puran Prasad Kurmi for their help in species identification in the field and at the Herbarium. We appreciate the comments from two anonymous reviewers, which have improved the quality and clarity of this manuscript. This work was financially supported by Swedish International Development Cooperation Agency (SIDA).

References

- Anonymous. 1994. Operational forest management plan for Nawal Paransi district (1995–2000). Forest Research and Survey Centre, Kathmandu.
- Arriaga L. 2000. Gap-building-phase regeneration in a tropical montane cloud forest of north-eastern Mexico. *Journal of Tropical Ecology*, **16**: 535–562.
- Babaasa D, Eilu G, Kasangaki A, Bitariho R, McNeillage A. 2004. Gap characteristics and regeneration in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology*, **42**: 217–224.
- Barik SK, Pandey HN, Tripathi RS, Rao P. 1992. Microenvironmental variability and species-diversity in treefall gaps in a subtropical broadleaved forest. *Vegetatio*, **103**: 31–40.
- Behera SK, Misra MK. 2006. Aboveground tree biomass in a recovering tropical Sal (*Shorea robusta* Gaertn. f.) forest of Eastern Ghats, India. *Biomass and Bioenergy*, **30**: 509–521.
- Bertrand B, Shachak M, Gutterman Y, Brand S. 1995. Patchiness and disturbance: plant community responses to porcupine diggings in the central

- Negev. *Ecography*, **18**: 410–422.
- Brokaw NVL. 1985. Gap-phase regeneration in a Tropical forest. *Ecology Letters*, **66**: 682–687.
- Brokaw NVL, Scheiner SM. 1989. Species composition in gaps and structure of a tropical forest. *Ecology*, **70**: 538–541.
- Bullock JM. 2000. Gaps and seedling colonization. In: Fenner, M. (eds) *Seeds: the ecology of regeneration in plant communities*, pp. 375–395. Wallingford UK: CABI Publishing.
- Chambers JC. 1995. Relationships between seed fates and seedling establishment in an Alpine ecosystem. *Ecology*, **76**: 2124–2133.
- Chandrashekhara U, Ramakrishnan P. 1993. Gap phase regeneration of tree species of differing successional status in a humid tropical forest of Kerala, India. *Journal of Biosciences*, **18**: 279–290.
- Clarke PJ, Allaway WG. 1993. The regeneration niche of the grey mangrove (*Avicennia marina*): effects of salinity, light and sediment factors on establishment, growth and survival in the field. *Oecologia*, **93**: 548–556.
- Connell JH. 1978. Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a nonequilibrium state. *Science*, **199**: 1302–1310.
- Dalling JW, Hubbell SP, Silvera S. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology*, **86**: 674–689.
- Deb P, Sundriyal RC. 2007. Tree species gap phase performance in the buffer zone area of Namdapha national park, Eastern Himalaya, India. *Tropical Ecology*, **48**: 209–225.
- Denslow JS. 1995. Disturbance and diversity in tropical rain forests: the density effect. *Ecological Applications*, **5**: 962–968.
- Denslow JS, Aaron ME, Sanford RE. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *The Journal of Ecology*, **86**: 597–609.
- Garwood NC. 1989. Tropical soil seed banks: a review. In: Leck, M.A., Parker, V.T., Simpson, R.L. (eds), *Ecology of Soil Seed Banks*. Academic Press, Inc., New York.
- Gautam KH, Devoe NN. 2006. Ecological and anthropogenic niches of Sal (*Shorea robusta* Gaertn. f.) forest and prospects for multiple-product forest management - a review. *Forestry*, **79**: 81–101.
- Gotelli NJ, Graves GR. 1996. Null models in ecology. Washington: Smithsonian Institution.
- Huang W, Pohjonen V, Johansson S, Nashanda M, Katigula MIL, Luukkanen O. 2003. Species diversity, forest structure and species composition in Tanzanian tropical forests. *Forest Ecology and Management*, **173**: 11–24.
- Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, de Lao SL. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science*, **283**: 554–557.
- Jackson JK. 1994. Manual of afforestation in Nepal, second edition: Forest Research and Survey Center, Kathmandu, Nepal.
- Lawton RO, Putz FE. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology*, **69**: 764–777.
- Pakeman RJ, Attwood JP, Engelen J. 1998. Sources of plants colonizing experimentally disturbed patches in an acidic grassland, in eastern England. *Journal of Ecology*, **86**: 1032–1041.
- Pande PK. 1999. Comparative vegetation analysis and Sal (*Shorea robusta*) regeneration in relation to their disturbance magnitude in some Sal forests. *Tropical Ecology*, **40**: 51–61.
- Pandey SK, Shukla RP. 2001. Regeneration strategy and plant diversity status in degraded Sal forests. *Current Science*, **81**: 95–102.
- Pitman NCA, Terborgh J, Silman MR, Nuez P. 1999. Tree species distributions in an upper Amazonian forest. *Ecology*, **80**: 2651–2661.
- Li QZ, Bogaert J, Nijs I. 2005. Gap pattern and colonization opportunities in plant communities: effects of species richness, mortality, and spatial aggregation. *Ecography*, **28**: 777–790.
- Rautiainen O, Suoheimo J. 1997. Natural regeneration potential and early development of *Shorea robusta* Gaertn.f. forest after regeneration felling in the Bhabar-Terai zone in Nepal. *Forest Ecology and Management*, **92**: 243–251.
- Richards LA, Coley PD. 2007. Seasonal and habitat differences affect the impact of food and predation on herbivores: a comparison between gaps and understory of a tropical forest. *Oikos*, **116**: 31–40.
- Runkle JR. 1982. Patterns of disturbance in some old-growth Mesic forests of eastern North America. *Ecology*, **63**: 1533–1546.
- Runkle JR. 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A., White, P.S. (eds.), *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, pp. 17–34.
- Schnitzer SA, Carson WP. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, **82**: 913–919.
- Stevens MHH, Carson WP. 1999. The significance of assemblage-level thinning for species richness. *Journal of Ecology*, **87**: 490.
- Tabachnick BG, Fidell LS. 2001. Using multivariate statistics, fourth edition. Needham Heights, MA: Allyn & Bacon.
- Tabarelli M, Mantovani W. 2000. Gap-phase regeneration in a tropical montane forest: the effects of gap structure and bamboo species. *Plant Ecology*, **148**: 149–155.
- Uhl C, Clark K, Dezzio N, Maquirino P. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology*, **69**: 751–763.
- Vetaas OR. 1997. The effect of canopy disturbance on species richness in a central Himalayan oak forest. *Plant Ecology*, **132**: 29–38.
- Webb EL, Sah RN. 2003. Structure and diversity of natural and managed Sal (*Shorea robusta* Gaertn.f.) forest in the Terai of Nepal. *Forest Ecology and Management*, **176**: 337–353.
- Whitmore TC. 1989. Canopy gaps and the two major groups of forest trees. *Ecology*, **70**: 536–538.
- Whitmore TC. 1996. A review of some aspects of tropical rainforest seedling ecology with suggestions for further enquiry. In: Swaine, M.D. (eds) *Ecology of Tropical Forest Tree Seedlings*. UNESCO/Parthenon, Paris/Canforth.
- Yu Dapao, Zhai Lianjiang, Dai Limin, Wang Qingli. 2006. Dynamics of dominant tree species in a forest ecotone on the northern slope of Changbai Mountain. *Journal of Forestry Research*, **17**: 216–220.
- Zang RG, Tao JP, Li CY. 2005. Within community patch dynamics in a tropical montane rain forest of Hainan Island, south China. *International Journal of Ecology*, **28**: 39–48.
- Zang RG, Wang BS. 2002. Study on canopy disturbance regime and mechanism of tree species diversity maintenance in the lower subtropical evergreen broad-leaved forest, south China. *Plant Biosystems*, **136**: 241–250.